

## Notes on Waterfall Swift *Hydrochous gigas*: II. Nestling plumage and phylogenetic relationships

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Waterfall Swift *Hydrochous gigas* occurs in montane Peninsular Malaysia, Sumatra, Java and possibly Borneo (see Part I, pp. 117–122). Originally placed in *Collocalia* (Hartert & Butler 1901), its taxonomic position is, however, still debated. For a *Collocalia*, Waterfall Swift is atypically large. Brooke (1970) introduced *Hydrochous* as a subgenus name, merely on the basis of literature information (without seeing a specimen or live bird), but later raised the name to genus level, with Waterfall Swift *Hydrochous gigas* as its sole member (Brooke 1972). Brooke's rationale was (1) the larger size of Waterfall Swift compared to other *Collocalia*, (2) its lack of echolocation ability (Medway & Wells 1969) in contrast to *Aerodramus*, and (3) its peculiar nesting sites, near or behind waterfalls (Somadikarta 1968, Becking 1971). The species was tentatively placed by him in the tribe Collocaliini of the subfamily Apodinae, following the general division of the Collocaliini into three genera: (a) dull-plumaged echolocators (*Aerodramus*), (b) dull-plumaged non-echolocators (*Hydrochous*) and (c) dull or glossy plumaged non-echolocators (*Collocalia sensu stricto*) (Brooke 1970, 1972). This division needs revision, however, because *Collocalia troglodytes* of the Philippines has recently been proven to echolocate (Price *et al.* 2004).

To obtain insight into its phylogenetic relationships, Lee *et al.* (1996) compared mitochondrial cytochrome-*b* DNA sequences of *Hydrochous gigas* with those of several related species. The Maximum Likelihood Tree and the constructed Bootstrap Consensus Tree indicated that *H. gigas* is probably closely related to *Aerodramus*, although its precise phylogenetic position is uncertain because most parsimonious trees placed *Hydrochous* variously within *Aerodramus*, but never as a sister taxon to that genus. Thomassen *et al.* (2003) repeated the analysis but screened for a larger section of mitochondrial cytochrome-*b* DNA (i.e. 1143 bp, rather than 406 bp) in *H. gigas* and several allies. Their resulting Bootstrap Consensus Tree placed Waterfall Swift between two *Aerodramus* species, *A. maximus* and *A. fuciphagus*, but closer to *A. maximus*. The Maximum Likelihood Tree revealed the same topology, except that *H. gigas* now grouped with the single *A. vulcanorum* specimen examined.

Thus, the precise phylogenetic relationships of the Waterfall Swift remained somewhat uncertain. It is remarkable, however, that both research groups uncovered evidence of a close relationship between *Hydrochous* and the echolocating *Aerodramus* species: *Hydrochous gigas* has been shown to lack echolocation capacity by experimentally letting a specimen fly in a dark room (Medway & Wells

1969). In a recent publication, Price *et al.* (2005) performed another DNA analysis (cytochrome-*b* gene) of the same *Hydrochous gigas* specimen studied by Lee *et al.* (1996), which was collected by me and was examined by all of these authors without my knowledge or consent. Price *et al.* (2005) considered *Hydrochous* to be sister to the Three-toed Papuan Swiftlet *Aerodramus papuensis* (see Somadikarta 1967). Moreover they concluded that both *Hydrochous* and *A. papuensis* are sister to all other *Aerodramus* swiftlets. Hence, under this arrangement these two species are removed from amidst the *Aerodramus* and are placed as basal to them all.

My aim here is to describe the morphology and nestling plumages of Waterfall Swift in their various stages, as these might shed some light on the phylogeny of the species.

## Methods

### Observations

Most observations of Waterfall Swift nestlings were made at a site in western Java, at a relatively low waterfall (c.25 m) in the River Cicewol (06°46'S, 106°56'E), on the south slope of Mt Salak, at an altitude of c.1,100–1,200 m. Permanent observation of the nests at this site was impossible due to access difficulties and the problem of disturbance (see Part I). During brief nest inspections, the nestlings that could be reached were examined for size, the presence or absence of feathers (semiplumes) and development of feather tracts (pterylae). Weight was measured using a Pesola balance. Colour descriptions of the naked parts and feathers (semiplumes, etc.) were matched using Ridgway (1912) and Smithe (1974) colour swatches. Black-and-white and colour photographs were made for reference. Most observations were made in 1977–78, supplemented subsequently by further observations at the same site.

Because of the laborious work of constructing the stagings to reach the nests, nest inspections were usually repeated only 2–3 times after the first examination. Re-inspection was usually at an interval of 7–10 days, weather conditions permitting. Less-accessible nests were generally only visited once. Age estimations were therefore rather approximate, especially as the age of a chick when first found was not precisely known. Despite such shortcomings and the rather restricted number of visits, the approximate ages of the chicks were estimated reasonably precisely by comparing different chicks. Where possible, they were checked in following years and supplemented with additional information from other nesting sites.

### Semiplume morphology

The 'pseudo-down' (semiplume covering) of Waterfall Swift nestlings was compared with that of Common Swift *Apus apus*. Feather structures were studied in detail at higher magnifications with the aid of a Wild M-5 stereomicroscope (enlargements 60–300×) and a Wild M-20 research microscope (300–600×), in unstained preparations in air, observed under cover glass. The semiplume of the

Common Swift nestling examined was from a bird found dead in a nestbox, at Bennekom, The Netherlands, containing two other, live nestlings. It weighed 14 g and had a wing-length of 38.3 mm, and was estimated to be *c.* 14 days old.

### **Anatomical study**

Because the course of the main arteries (carotid arteries) in the neck and thorax of Apodiformes (Apodidae) is important for a judgment on their phylogeny, these were studied in several alcohol specimens of *Hydrochous gigas* (Java) and *Collocalia linchi* (Java), and in fresh (frozen) specimens of *Apus apus* (Netherlands). Attention was also paid to the feet of *H. gigas*, i.e. the grip, and to the number of phalanges in the different digits, compared to those in other swift species.

### **Photographic records**

As it was difficult to photograph the nestlings *in situ* on primitive ladders or scaffolds, the nestlings were briefly removed from the nests and photographed in a empty nest of the species at the foot of the fall, and afterwards immediately returned to their nests. The recently hatched young featured in Fig. 1 was found dead in its nest at another colony.

## **Results**

### **Post-hatching development**

Four different developmental stages of the nestling were recognised.

#### **Newly hatched chick**

As in all Apodidae, the hatchling is naked and blind (Figs. 1–2, two different chicks). A well-developed whitish egg tooth is conspicuous at the distal upper ridge of the upper mandible of the pinkish bill. The lower mandible protrudes somewhat beyond the upper mandible due to a second egg tooth-like structure or tubercle at the distal end of the lower mandible. This was pointed out to be a second egg tooth (C. T. Collins *in litt.* 2005). The skin is pinkish (Smithe: Salmon Color/Pink [6/7]; Ridgway: Pale Flesh Color (Pl. XIV)), with a very slight plumbeous or greyish tinge (Smithe: close to Light Neutral [85]; Ridgway: Light Varley's Gray [Pl. XLIX]). This greyish tinge is darker on the head, back and wings. The pinkish feet are soft and rather large for the size of the chick (Fig. 1). Newly hatched chicks weighed *c.* 2–3 g and had a body length of *c.* 3.5 cm. A large throat pouch is visible, an adaptation for taking food boluses. At this stage, the parents brood the chick continuously, and leave it only reluctantly if disturbed. The naked chick clearly requires nearly continuous parental cover for its insulation.

#### **Chick of 4–8 days**

At this age chicks are still completely naked and their eyes closed, but on the back slightly darker plumbeous feather tracts are visible below the epidermis, one dorsal (spinal tract) and one somewhat laterally on each side (femoral tract) (Fig. 3). In



Figure 1. Recently hatched Waterfall Swift *Hydrochous gigas* nestling (Jan-Hendrik Becking)



Figure 2. A few days-old nestling of Waterfall Swift *Hydrochous gigas* (Jan-Hendrik Becking)

addition, within the apteria many small dark spots appear (the underlying follicles of the down-like semiplumes). The coronal and occipital tracts of the body also become more prominent as dark grey (Smithe: Medium Neutral Gray, 84) areas or lines. The underside and anal region are still very pale greyish pink, and no underlying feather tracts are visible. Subsequently, the plumbeous grey back and head become darker (Smithe: Dark Neutral Gray/Medium Neutral Gray, 83/84), whilst the pinkish bill acquires a blackish tip and darker upper rim. The skin of the orbits of the protruding eyes also becomes darker, as does the skin of the tibia and femur and at the upper rim of the wing. The base of the broad bill, however, is pale flesh pinkish, even almost white. At this stage the skin does not cover the body smoothly but is rather wrinkled or folded, especially on the back and body-sides. The gape and palate are vivid flesh-pink, the tongue pinkish with a greyish tip. When 6–7 days old the chick is *c.*5 cm in length (head width 15.6 mm), but with its neck stretched—as when begging—can reach 6.5–7.0 cm. It weighs *c.*9.3 g, i.e. about 3–4 times its weight when newly hatched (2–3 g, *N*=5).

### **Chick of 10–15 days**

A ‘downy’ semiplume covering sprouts on the back from the developed follicles visible earlier, giving the chick what looks like a coat of down (Fig. 4). The semiplumes sprout mainly from the apteria, but are often denser at its borders, and also develop on the head and upper chest. The chick starts to open its eyes, but if exposed to brighter sunlight immediately closes them. When handled the chick always tries to turn its head towards the shade. The growth of the covering is rather fast on the dorsal side, but far slower on the ventral side. The semiplumes are greyish black (Smithe: Dark Neutral Gray, near 83) and when fully grown measure *c.*10 mm. The first wing- and tail-feathers appear, still enclosed by their sheaths.

### **Chick of *c.*17–22 days**

Although the semiplumes are still prominent, the growth of the primaries and secondaries, followed by the greater coverts, is rather rapid. As these feathers are still in sheath, the chick acquires a pin-cushion-like appearance, an image strengthened because the sheaths of the greater coverts and those of the carpal edge often point obliquely sideways from the wing (Fig. 5). Later, the secondaries and upperwing-coverts start to open their vanes at the tips, whilst the primaries are still enclosed within their sheaths.

There are indications that near the end of the ‘downy’ semiplume stage these semiplumes are very loosely implanted in the skin. A chick of this age found recently dead in a nest, which I tried to preserve as a specimen, lost most of its semiplumes during preparation, although I took utmost care to prevent this. The semiplumes which became detached during the skinning process were not still ensheathed, but full grown.

At a late stage the dense semiplumes become mixed with another type of unique feathers, which sprout from other follicles. They are more like normal contour



Figure 3. A 7–9-day-old nestling of Waterfall Swift *Hydrochous gigas* showing the somewhat contrasting darker pterylosis tracts regions on the back, and (in the upper left corner) the copious quantities of whitish gelatinous saliva used to bind the nest to the rock (Jan-Hendrik Becking)



Figure 4. A c.10–15-day-old nestling with semiplumes and its first contour feathers, the latter still in an early stage within their sheaths (Jan-Hendrik Becking)

feathers in having a loose-webbed base, followed by a short closed vane and ending in a more or less semiplume-like apex (Fig. 6d). The plumulaceous bases (of these new feathers) bear blackish-grey barbs identical to the initial semiplumes, but the closed vane is buffish yellow (Smithe: Cream Color, 54) and the grey semiplume-like endings have fine yellowish tips, affording the chick a somewhat variegated appearance, which is intensified when it raises its back feathers and appears bristly (Fig. 5).

A second wave of largely plumulaceous feathers arising from other follicles is exceptional and conflicts with any moult system known. Moreover, moult is described as a periodic shedding and replacement of feathers (Campbell & Lack 1985), and the follicles should persist and produce a series of feathers from each during the course of the bird's lifetime. This would mean that the downy semiplumes are overgrown by incoming contour feathers and thus disappear from sight, but are not lost or dropped. However, when I removed the contour feathers from an adult alcohol specimen of *H. gigas* I found very few 'downy feathers' below. This is a puzzle that requires solution. A second set of semiplumes is certainly very exceptional and unknown for any species of swift, but has been reported in other birds. It is unknown or disputed whether the moult pattern of contour feathers in birds can be applied for the semiplumes occurring in the apteria.



Figure 5. A c.17–20-day-old nestling showing the unique type of feathers (intermediate) between semiplumes and contour feathers. When these feathers are raised the nestling acquires a bristly appearance (Jan-Hendrik Becking)

It has been suggested that I had to examine the semiplume downy cover (and follicles) in the Waterfall Swift chicks more precisely, but this can not be done in a living chick without doing it severe harm. This can only be done in a dead chick, but I refrained from to sacrifice a chick for this purpose as the scope of this investigation was to follow its development<sup>1</sup>.

### Nestling of c.25–45 days

At this stage nestlings were rarely handled, because they were rather sensitive to disturbance. Moreover, they tended to grip with their feet very strongly to the underlying nest material and were therefore difficult to remove. The chicks at this stage are covered with sooty grey-brown contour feathers (Smithe: between Blackish Neutral Gray (82) and Dark Neutral Gray (83); Ridgway: Deep Slaty Brown, Plate L), paler on the underside and darker on the upperside, and with extensive white at their bases, particularly on the back, belly and flanks. Often this basal white is not completely concealed, giving the nestlings a somewhat spotted appearance. Completely white small underlying feathers can also be found on the back and belly, but apparently only very few semiplumes under these first contour feathers, as far as could be determined. It is noteworthy that Waterfall Swift nestlings at this age lack the pale greyish fringes to the primaries, secondaries and other contour feathers well known in older nestlings or juveniles of *Apus*, and also present in some Cypseloidinae (Marín & Stiles 1992). I estimate that nestlings leave the nest 48–55 days after hatching.

### Description of the semiplumes

Unlike true natal down (neossoptiles), semiplumes are modified loose-webbed contour feathers (teleoptiles). Semiplumes have a definite rachis but no hamuli on the barbules, and therefore cannot produce a firm vane (Nitzsch 1840, Chandler 1916, Van Tyne & Berger 1971). The semiplumes of *Hydrochous gigas* are blackish grey (Smithe: Medium Neutral Gray/Dark Neutral Gray, near 84/83) and thus distinctly greyer than the uniform sooty-black (Smithe: Blackish Neutral Gray, 82) semiplumes of *Apus apus* studied for comparison.

As mentioned, there are two successive types of plumulaceous feathers. The first (Fig. 6a) develops from the naked chick. These are more or less spherical in form and usually c.6–10 mm long, occasionally 12.5 mm when fully grown. Smaller ones may also occur, 5–6 mm long. The semiplumes of *H. gigas* have no aftershaft at their base (Fig. 6a), unlike the semiplumes of *Apus apus*. At low magnification the

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<sup>1</sup> From the observation that there are very few semiplume feathers in an adult it may be concluded that they are lost and not replaced by new ones. It may be also that the dermal papilla at the base of the follicle is dormant for a time. I have the impression that the same sequence of processes, from 'downy cover' to juvenile and adult plumage, occurs in *Apus apus*. Through the courtesy of the Apus Working Group Netherlands, I have been given some chicks (found dead in the nest) and semi-adults and adults from Bird Shelters (mainly traffic victims), and with this material I hope to solve this plumage problem.



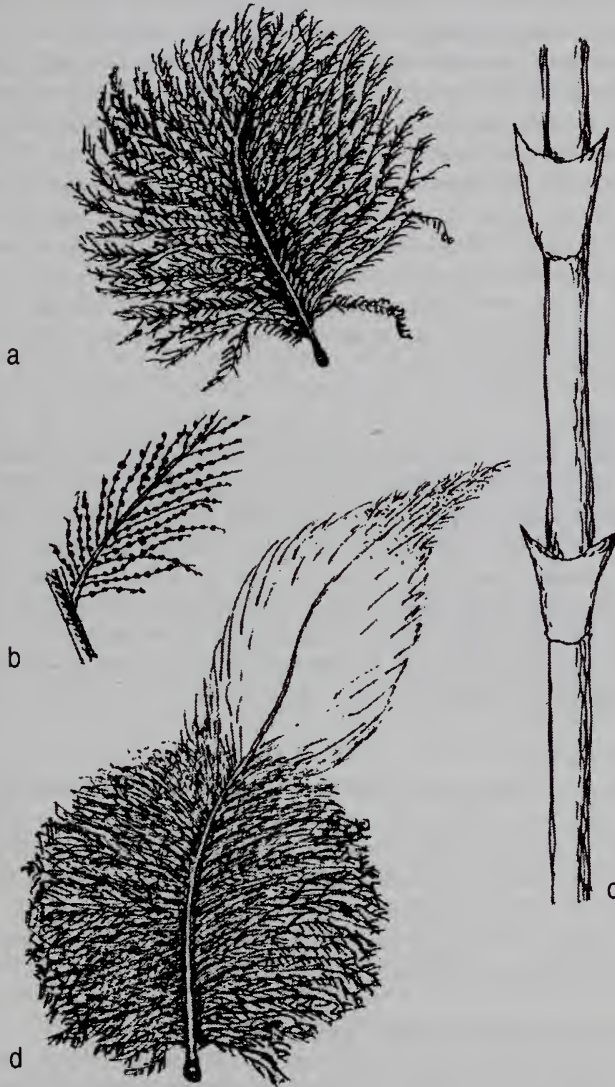


Figure 6. Drawings of semiplumes, etc. of Waterfall Swift *Hydrochous gigas*: (a) 'downy feather' (semiplume) of the first type; (b) a semiplume of the first type at low magnification, showing a chain of regularly spaced black dots (nodes) within the clear barbules; (c) a barbule of a semiplume of the first type at higher magnification, showing small thickenings (nodes or barbicels), which usually bear distally oriented spiny projections (prongs); and (d) a feather of the other unique type, being intermediate between a semiplume of the first type and a contour feather; it has a plumulaceous base followed by a short closed vane and ends in a fine semiplume-like apex (*del.* Jan-Hendrik Becking)

barbules of the semiplumes of Waterfall Swift appear transparent with a chain of regularly spaced black dots like a string of beads (Fig. 6b), whereas the barbules of *A. apus* are uniformly blackish without hyaline interspaces. At higher magnification (500–600×), the black dots in the barbules proved to be dark pigmented thickenings or projections, so-called nodes (Rosalind & Grubh 1987, Rajaram 2002). These are regularly spaced along the barbules with an internodal distance of *c.* 9–10  $\mu\text{m}$ . They are broadest towards the tip and usually have spiny projections, or ‘prongs’ (Fig. 6c).

The second type of feathers, being more like contour feathers, possess a partially closed vane and are about twice as long as the first type, *c.* 18–19 mm, width 11–12 mm (Fig. 6d). When both types are observed closely with a magnifying glass or stereomicroscope, they are seen to have yellowish tips, a feature absent in the semiplumes of *Apus apus*.

### **Anatomical study**

The Cypseloidine swifts, which in breeding in association with waterfalls and also in their size, are very similar to that of *Hydrochous gigas*. These Cypseloidine swifts have, however, two carotid arteries (Glenny 1953, 1955), as in most birds, which is supposed to be the primitive condition. In *H. gigas* I found only one carotid artery in the laevo, i.e. sinistra, position connected to the heart, as in *Collocalia linchi* and *Apus apus*. The latter is regarded as the derived condition. In contrast to the feet of representatives of the genus *Apus* (Stresemann 1934), those of *H. gigas* are anisodactyl without any reduction of phalanges in the toes. This means its feet have 3, 4 and 5 phalanges for digits 2, 3 and 4, respectively.

### **Egg tooth development**

The observed second egg tooth on the lower mandible of the Waterfall Swift is not unique to the species, having been found in other swifts. Collins & Naik (1975) described it for *Apus nipalensis*, of the subfamily Apodinae, in India. Moreover, it is reported (Collins 1968) for Short-tailed Swift *Chaetura brachyura* and Chestnut-collared Swift *Cypseloides rutilus* of the subfamily Cypseloidinae. Although of interest, the presence of two egg teeth in newly hatched *H. gigas* chicks throws no light on the phylogenetic relationships of Waterfall Swift.

### **Breeding biology compared to other swift species**

Based on my observations, the breeding season of Waterfall Swift in western Java appears to last from September to January, sometimes until February/March (due to replacement clutches), coinciding with the rainy season, when termites, preferred food of Waterfall Swift, conduct mating flights and are readily available (pers. obs.). Termites were also found to be usually the sole prey in stomachs of this species examined by Max Bartels Snr. (notes held in the Leiden Museum). Moreover, the few stomachs (five), which I examined (in the rainy season) were distinctly enlarged and crammed with remains of termites. The estimated fledging period of

45–55 days is slightly shorter than that of the similar-sized and ecologically similar White-chinned Swift *Cypseloides cryptus* of the Neotropics (Marín & Stiles 1992, Chantler 1999). There is also a great similarity between the breeding biology of *Hydrochous gigas* and Cypseloidine swifts of the New World in respect of site preference, nest type and, for some species, even clutch size (single-egg clutches). *H. gigas* and Cypseloidine swifts are not, however, closely related, as fundamental differences exist between them (see above). The similarity is doubtless due to convergent evolution, resulting in their adaptation to the same very special nesting requirements.

## Discussion

The discovery of a 'down-like' semiplume nestling plumage in *Hydrochous gigas* nestlings is surprising, as it is absent in all species considered its closest relatives, i.e. *Collocalia* and the echolocating *Aerodramus*. It is also lacking in the tribe Chaeturini (following Brooke 1970). Such plumage is, however, present in the subfamily Cypseloidinae of the New World, which also shows a great resemblance to Waterfall Swift in morphology, habits and nest-site choice, selecting sites close to running water or waterfalls, and construct similar types of nest (Becking 1971, Marín & Stiles 1992).

The semiplume covering of young nestlings of *Hydrochous* is probably an adaptation to its breeding in cool damp environments, assisting the insulation and thermoregulation of the chick, a view supported by some of my field observations. Newly hatched nestlings of Waterfall Swift were near-continuously brooded by one adult, but when the semiplume plumage was fully developed they were left unattended for shorter or longer periods. A similar suggestion regarding the function of down-like plumage was also made for Cypseloidine nestlings by Legg (1956) and Collins (1963).

The formation of a second plumulaceous covering, as reported for *H. gigas*, appears to be unique in swifts, but a second, successive coat of nestling down was first noted by W. E. Clark (1906) in penguins (for neossoptiles), and later recorded in most owls as well as certain other groups. These, however, are from the same follicle and are extruded on the incoming contour feathers (teleoptiles).

Environmental circumstances may not be the only explanation for the forming of a down-like covering. Of the two species of *Cypsiurus* palm swifts living under similar climatic conditions to each other, with the same life histories and nest-site choice, and building the same type of nests, the chicks of African Palm Swift *C. parvus* are densely covered with semiplumes (Schuster 1912, Moreau 1941, Collins 1965). Chicks of Asian Palm Swift *C. balasiensis*, however, are completely naked until the contour feathers appear (Hails & Turner 1984; pers. obs.). This suggests the presence of an essential genetic factor, playing a role in the growth (i.e. presence or absence) of semiplumes on chicks, in addition to environmental factors already mentioned.

Teleoptile semiplume plumage is also present in chicks of *Apus apus* and Alpine Swift *Tachymarptis melba*, which were originally cliff breeders in a cool climate (Glutz von Blotzheim & Bauer 1980, Cramp 1985). Unlike *Apus apus* and *Tachymarptis melba*, however, which have a so-called pamprodactyl foot (but see Collins 1983) with only three phalanges in digits 2–4 (Stresemann 1934), those of *H. gigas* are anisodactylous with no reduction in the phalanges (see above). The subfamily Cypseloidinae similarly have the normal avian anisodactylous condition, as does the enigmatic African genus *Schoutedenapus*. For precisely this reason, Scarce Swift *Schoutedenapus myoptilus* underwent a generic name change from its original *Apus myoptilis* (Salvadori 1888, De Roo 1963). There is a chronic lack of available data for *Schoutedenapus*: its breeding is unknown, and little is known of its behaviour and distribution either. The enigmatic position of both *Schoutedenapus myoptilus* and *Hydrochous gigas* was reviewed by Collins (2000).

It is striking that the two *Cypseloides* with the same mass as Waterfall Swift (35.79 g,  $N=19$ , pers. obs.), namely *C. cryptus* (35.27 g,  $N=13$ ) and *C. niger* (35.71 g,  $N=16$ ), also lay only a single egg (Legg 1956, Marín & Stiles 1992). The much smaller *C. rutilus* (21.32 g,  $N=139$ ) has a two-egg clutch (Collins 1968, Marín & Stiles 1992). There may be a relation between body mass and nesting behaviour in these species. A close relationship between Cypseloidine swifts and Waterfall Swift is unlikely, for several reasons. All Cypseloidine swifts have a diastataxic wing (H. L. Clark 1906, Stephan 1970) and two carotid arteries like most birds (Glenny 1953, 1955), whereas some Apodini (*Collocalia bartschi* and *Aeronautus andecolus*) have only one laevo-carotid artery (Glenny 1953, 1955). As mentioned, I found only one carotid artery, in the laevo, i.e. sinistra, position, in Waterfall Swift, *Collocalia linchi* and *Apus apus*. Moreover, Cypseloidine swifts possess no active salivary glands and therefore do not use saliva for nest building (Johnston 1961, Marín & Stiles 1992, Marín 1997). Waterfall Swift, however, uses copious saliva for nest attachment and some to bind the nest material, especially the rim. This saliva is originally white or opaque whitish gelatinous (see Fig. 3), but soon becomes black, particularly in older nests and especially in museum specimens. It is, therefore, frequently overlooked. A further difference is the use of mud for nest building: in Cypseloidine swifts it may comprise a considerable proportion (44–89%) of nest material (Marín & Stiles 1992), whereas this habit is entirely absent in Waterfall Swift (Becking 1971). Finally, there are some osteological differences, particularly in respect of the skull (Orr 1963).

## Conclusions

The resemblance of Waterfall Swift to Cypseloidine swifts is probably due to convergence and related to their similar breeding habits. However, the formation of a second semiplume-like covering appears to be unique to Waterfall Swift. Conversely, differences in nestling plumage between Waterfall Swift and various *Collocalia* and *Aerodramus* species are probably due to differences in nesting habits, rather than large phylogenetic distance. It is unknown what phylogenetic

importance should be attached to the difference in echolocating capabilities between Waterfall Swift and various *Aerodramus* species. DNA studies of *H. gigas* and associated species to date have been inconclusive, and the precise taxonomic position of *H. gigas* remains to be determined.

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